Behavioural Processes 121 (2015) 54–62

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Context-dependent third-party intervention in agonistic encounters of male Przewalski horses

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ARTICLE INFO

Article history:
Received 22 June 2015
Received in revised form 2 October 2015
Accepted 10 October 2015
Available online 23 October 2015

Keywords:
Equus ferus przewalskii
Group conflict
Rank orders
Social bonds
Social control
Third-party intervention

ABSTRACT

One mechanism to resolve conflict among group members is third party intervention, for which several functions, such as kin protection, alliance formation, and the promotion of group cohesion have been proposed. Still, empirical research on the function of intervention behaviour is rare. We studied 40 cases of intervention behaviour in a field study on 13 semi-wild bachelor horses (*Equus ferus przewalskii*) in (a) standard social situations, and (b) when new horses joined the group (i.e. introductions). Only interventions in agonistic encounters were analysed. Eight of 13 animals directed intervention behaviour toward threatening animal in agonistic encounters of group members. One stallion was particularly active. The stallions did not intervene to support former group mates or kin and interventions were not reciprocated. In introduction situations and in standard social situations, the interveners supported animals which were lower in rank, but targeted, threatening animals of comparable social rank. After introductions, stallions received more affiliative behaviour from animals they supported and thus appeared to intervene for alliance formation. In standard social situations, interveners did not receive more affiliative behaviour from animals they supported and may primarily have intervened to promote group cohesion and to reduce social disruption within the group.

1. Introduction

Conflict among individual group members poses a severe threat to the cohesiveness and integrity of social groups and therefore needs to be resolved (Bernstein, 1976; de Waal, 1977; Ehardt and Bernstein, 1992; Flack et al., 2005, 2006). Third-party interventions may provide one of several ways to maintain group stability (Aureli and de Waal, 2000; Smith et al., 2010), when interveners interrupt interactions between initiators and recipients through direct physical contact, interposition, or threats (Widdig et al., 2006; Jennings et al., 2009; Smith et al., 2010; Fig. 1).

Especially when animals intervene in agonistic encounters of group members, third-party intervention is potentially costly for the intervener, who risks physical injury and invests energy and time in scanning group behaviour (Clutton-Brock, 2009; Smith et al., 2010). Nevertheless, the consistent and widespread occurrence of this behaviour in numerous species of animals including humans suggests that interveners benefit from their behaviour. Benefits may be indirect and direct fitness gains.

First, interveners which support distinct animals may support or protect kin, as in primates (Hamilton, 1964; Gouzoules and Gouzoules, 1987) and spotted hyenas (*Crocuta crocuta*) (Zabel et al., 1992; Smith et al., 2010). Second, animals may attempt to secure the reciprocation of aid for future encounters from the individual they support through intervention (Trivers, 1971), as shown in many primate species (de Waal and Luttrell, 1988; Silk, 1992; Schino et al., 2007), as well as in coaties (Romero and Aureli, 2008). Third, by supporting particular animals interveners may support or win alliance partners, as in male baboons (*Papio* spp.), female rhesus macaques (*Macaca mulatta,* Noë et al., 1991; Noë, 1992; Noë and Hammerstein, 1994, 1995), spotted hyenas (*Crocuta crocuta*) (Zabel et al., 1992; Smith et al., 2010), zebras (*Equus quagga*, Schilder,

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http://dx.doi.org/10.1016/j.beproc.2015.10.009
0376-6357/

1990) and domestic horses (*Equus caballus*, VanDierendonck et al., 2009; Schneider and Krueger, 2012; Granquist et al., 2012). The formation of alliances is a frequent strategy in group living animals to gain mutual access to resources, such as grooming partners, mating partners, food, shelter, etc. (Noë and Hammerstein, 1994; Connor, 1995; Schülke et al., 2010; Schneider and Krueger, 2012), to reduce predation pressure and to improve reproductive success (Cameron et al., 2009). Interventions of the first three causalities may be displayed by animals of any social rank as described for chimpanzee females, which were of middle rank (de Waal, 1982).

Fourth, middle to high ranking animals may intervene in agonistic encounters of group members without supporting specific animals. This may promote group cohesion (Bernstein, 1976; Ehardt and Bernstein, 1992) through reducing tension (de Waal, 1977) and social disruption within the group (Flack et al., 2005, 2006; Jennings et al., 2009; von Rohr et al., 2012) and stabilize the group's social rank order (Packer, 1977; Flack et al., 2005, 2006).

We would expect that only a few group members intervene in agonistic encounters of group members, as they run high risks of physical injury (Frank, 1996). Indeed, in primates, including humans, only certain members of a social group take over the social role of an intervener (i.e., specified social context; Hinde, 1978; Ehardt and Bernstein, 1992; Salmivalli et al., 1996; Flack et al., 2005, 2006 on Rohr et al., 2012). Such interveners may engage exceedingly in social activities of the group, as suggested by Granquist et al., 2012.

Here, we study interventions in agonistic encounters among 13 stallions in a semi-wild bachelor group of Przewalski horses (*Equus ferus przewalskii*) kept in semi-natural conditions in Tennenloher Forst, Germany. In horses, male offspring disperse from their natal groups, either singly or together with related and unrelated group mates (Tilson et al., 1988; Houpt and Boyd, 1994; Zharkikh and Andersen, 2009). They remain in bachelor groups until maturity. When mature stallions take over harems, they guard the harem mares and their offspring (Berger 1986). Przewalski horses have been observed to support individuals that are attacked by other group members (Tilson et al., 1988; Houpt and Boyd, 1994; Zharkikh and Andersen, 2009). It was suggested that interveners benefit through kin protection (Boyd, 1988; Houpt and Boyd, 1994; Zharkikh and Andersen, 2009) or alliance formation (Tilson et al., 1988).

For the present study, interactions were recorded both in standard social situations and during the introduction of new animals. We predicted that:

(a) Only a few group members display interventions (de Waal, 1982; Clutton-Brock and Parker, 1995; Flack et al., 2005, 2006; von Rohr et al., 2012),
(b) Interveners protect former field-mates with whom they might have formed short term alliances for protecting themselves or their resources in the past, but they do not support kin. This is because horses recognize and memorize individual group mates (Proops et al., 2009; Krueger and Flauger, 2011), but have never been shown to recognize unfamiliar kin,
(c) Intervention is not reciprocal, as reciprocal aid has not been shown in horses or other ungulates (Jennings et al., 2009),
(d) Interveners are of high social rank and rise faster in the social hierarchy than the animals they target (de Waal, 1992; Clutton-Brock and Parker, 1995; Flack et al., 2005, 2006),
(e) Interveners are highly social (Granquist et al., 2012) and exchange more affliative than agonistic behaviour with their group members,
(f) Interveners preferentially support alliance partners or intervene to form long lasting alliances for future, mutual resource protection (de Waal, 1992; VanDierendonck et al., 2009; Schneider and Krueger, 2012; Granquist et al., 2012).

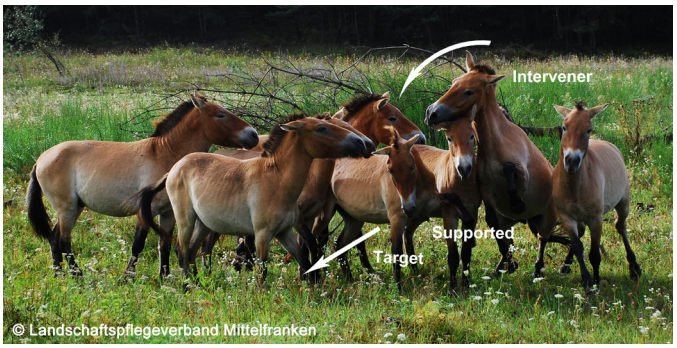

Fig. 1. 3rd party intervention. The picture shows an agonistic encounter in a high aggression situation when a new horse joined the group. An intervening horse (i.e., the intervener) supports a recipient of a front leg kick (i.e., the supported, the new horse) by threatening the initiator of the encounter (i.e., the target). Arrows depict the movement direction of the third-party intervention participants.

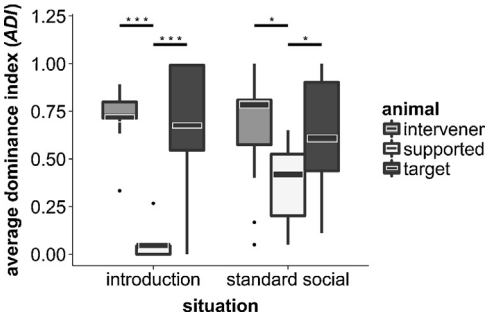

Fig. 2. Differences in social rank between intervener, supported and targeted animals. The rank was calculated from an average dominance index (*ADI*). Boxplots show the median, interquartile range, minimum, maximum and outliers (dots). Social ranks between intervener and supported horses differ for introduction and standard social situations. *** $P < 0.001$, * $P < 0.05$ (after sequential Bonferroni correction).

2. Material and methods

2.1. Animals and enclosure

We observed 13 male wild horses (*Equus ferus przewalskii*) kept by Landschaftspflegeverband Mittelfranken in semi-wild management in a 50 ha enclosure of forest and grassland in Tennenlohe near Erlangen, Germany. They had free access to water, vegetation, and received additional hay and horse feed in winter. For controlling the horses' well-being, they were observed by park rangers daily.

The horses had been raised in the zoos of Nuremberg and Munich, Germany, and were transferred to the enclosure when they were one or two years old, and stayed there until maturity. During the study period the ages of the individuals ranged between 1 and 8 years (Table 2). At the study area the horses formed one group, consisting of six to ten individuals and changing in composition due to immigrations (5 horses) and emigrations (6 horses) during the observation period. New males were introduced, singly or in pairs in April 2008, May 2009, June 2009 and July 2009. Twelve of the observed horses were related to up to three others (Table A.1) and five horses were familiar with one or two other horses from their previous housing (Table A.2). Pairs of horses for which familiarity status was unknown were excluded from the analysis of the effect of familiarity on interventions.

The composition and size of the study group resembled that of unstable, feral bachelor horse groups (Tyler, 1972; Berger, 1986; Tilson et al., 1988; Houpt and Boyd, 1994; Linklater et al., 2000), where male horses switch between staying with harems or bache-